SPECIES OF THE NEMATODE GENUS STRONGYLOIDES PARASITIC IN DOMESTIC SWINE 1

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INTRODUCTION

The object of this paper is to clear up the existing confusion and uncertainty with reference to the specific identity of the nematodes of the genus Strongyloides parasitic in domestic swine. Strongyloides suis has been used by certain workers to designate a distinct zoological species, and by others it has been used merely as a convenient host designation for Strongyloides from swine. ably the majority of helminthologists who have expressed an opinion on this subject have regarded S. suis as a synonym or as a probable synonym of S. papillosus of sheep. The investigations reported in this paper, together with a study of the literature relating to Strongyloides of swine, have shown that two species of this nematode genus have been reported from these host animals. One species, which is the form involved in an extensive account of the pathogenicity of Strongyloides to young pigs by Reisinger (14),2 is considered in this paper as S. suis, and the other species, which presumably is the form which many helminthologists have considered identical with S. papillosus, is regarded as new.

REVIEW OF LITERATURE

Reisinger (14), Sandground (15), Baylis (1), and other workers who have studied Strongyloides have overlooked the fact that Pagenstecher (9) recorded Strongyloides from pigs, presumably for the first time, and that his observations antedated those of Grassi (3) and Lutz (7). Lutz has erroneously been credited with being the first to report Strongyloides from swine. Pagenstecher (9) records small, slender worms, consisting entirely of female specimens, from the small intestines of pigs. He recognized these worms as related to Anguillula (synonym, pro parte, of Strongyloides) and described their morphology in considerable detail, listing all the salient generic characters of the genus Strongyloides. Pagenstecher says that the ovary is short in young specimens and that it increases in size as the worms grow older, finally becoming twisted in loops around the intestine, anteriorly and posteriorly, a character which has been figured and described with reference to Strongyloides of swine by later workers. Grassi (3) reports that animals other than man harbor Anguillula

intestinalis (as used by Grassi this name is a synonym of Strongyloides stercoralis, parasitic in man); he records these parasites from swine, rabbits, and weasels, and he also refers to their occurrence in cows, chickens, cats, sparrows, and mice, and notes their absence in several species of amphibians and reptiles which he examined.

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 Reference is made by number (italic) to "Literature cited," p. 22.

that the forms from the different hosts differ in certain respects, especially in size, and expresses the opinion that they belong to the

same genus.

The same author (4) used the name Rhabdonema longus for the form from sheep and reiterates the opinion that the same species also occurs in the rabbit, the weasel, and the pig. He says that the parasitic female is 7 mm. long and notes that in the free-living generation of R. longus the females outnumber the males to the extent of 1,000 to 1. He also notes that the free-living females of this species often

die without having copulated.

Lutz (7), apparently unaware of previous records of the occurrence of Strongyloides in pigs, reports observations on these nematodes from swine, based on a study of the parasitic females which he obtained on necropsy from a pig in Brazil, as well as observations on the free-living males and females which he cultured in the feces obtained from the same host animal. Lutz says that he recognized the similarity of these forms to those of Anguillula stercoralis, from man, as described by Perroncito (10), noting, however, certain differences in size. He states that the parasitic females from the swine are about 1 cm. long and that the free-living males and females, which he obtained from fecal cultures in approximately equal proportions, are twice the size of those cultured from human feces. He also notes that the eggs of the pig Strongyloides hatch outside of the body, whereas those of the human form hatch before they are eliminated with the feces.

Von Linstow (6) uses the name Strongyloides suis for the first time and erroneously credits Lutz with being the author of this name. Von Linstow not only proposed a new name, but at the same time that he proposed it he also relegated it to the synonymy, as he lists S. suis as a synonym of S. longus (Grassi and Segré) and gives the following hosts for this species: Ovis aries, Sus scrofa, Lepus cuniculus, Foetorius vulgaris, and Mus decumanus. Aside from listing the hosts of S. suis and stating that it is 6 mm. long, he gives no description. S. longus (Grassi and Segré) is regarded at the present time as a synonym of S. papillosus.

Perroncito (10) reports Strongyloides from swine, especially from young pigs, and gives an account of the pathogenicity of these parasites. His paper contains no data with reference to the morphology

of the worms, which he does not name specifically.

Ransom (13) reports for the first time, the occurrence of Strongy-loides in pigs in the United States. He makes the following statement with reference to the specific identity of Strongyloides from American swine:

The parasite of the pig, which has been identified as Strongyloides longus (=S. papillosus) by European observers, is probably Strongyloides suis. This species has been found a number of times in pigs at the Bureau of Animal Industry Experiment Station, Bethesda, Md.

Railliet (11) lists Strongyloides suis (Leuck.) from swine. The present writers have been unable to trace any reference to the specific name suis used by Leuckart in combination with any synonyms of the genus Strongyloides.

Reisinger (14), in an extensive paper on the pathogenicity of Strongyloides to young pigs, gives very valuable clinical data and figures and describes a species of Strongyloides for which he uses the

names S. suis and S. longus interchangeably. As will be shown later, the morphology of the worms as figured and described by Reisinger differs in several important respects from that of the worms which have been collected from pigs in Bethseda, Md., and studied by the writers.

Marotel (8) describes a chronic enteritis in pigs due to Strongyloides suis. His paper is not available to the writers. The abstracts of this paper which have been consulted contain little information in regard to the morphology of the worms, the parasitic female being described only as from 3 to 4 mm. long by 30μ to 40μ wide.

Fiebiger (2) regards Strongyloides from pigs as identical with S. longus of sheep and rabbits. His figure of this species from pigs agrees with Reisinger's figure of S. suis.

Hall (5) recognizes Strongyloides suis as a valid species, listing S. longus (pro parte) as its synonym, and noting for the first time that the forms found in the eastern part of the United States do not agree with the description of S. suis as given by European helminthologists.

Sandground (15) questions the validity of Strongyloides suis and states that he examined several specimens (parasitic females) of Strongyloides from swine obtained from the helminthological collection of the Bureau of Animal Industry, and found that the ovary is twisted

around the intestine, as in S. papillosus. He says:

The only possible distinction that could be made between these specimens and S. papillosus would be on the basis of a more acutely pointed tail in S. suis; but as this character is very variable, the distinction between S. suis and S. papillosus on morphological grounds is uncertain.

Sandground's statement with reference to the variability of the shape of the tail in the two species might be interpreted as implying that the forms from pigs and sheep overlap with regard to this morphological feature. As will be shown later, such overlapping has not been observed by the writers. On the contrary, the shape of the tail is remarkably constant for the sheep form as well as for the form from pigs, the difference between the two being very distinct and striking.

Baylis (1) says:

S. suis von Linstow, 1905, a form originally recorded by Lutz in 1885 from the pig, appears to be a very doubtful species, and is probably identical with S. papillosus.

There are several additional references to Strongyloides in swine which, in the main, are repetitions of opinions expressed by other workers and supported by little, if any, original observation or

critical examination of published data.

It is evident from this summary of the literature with reference to Strongyloides in swine that the views expressed by Grassi with. reference to the specific identity of the sheep and swine forms have largely prevailed and that a number of later workers who have accepted these views have not supported them with morphological evidence based on original observations. A conspicuous exception is Ransom (13), who was familiar with the forms from the two hosts and did not consider them identical. It should also be noted that Hall (5) observed the discrepancies between descriptions by European investigators of the morphology of Strongyloides from swine and the forms from swine occurring in the eastern part of the United States

with which he was familiar, and that he also recognized the fact that S. longus is a synonym of S. suis only so far as the former has reference to forms from pigs.

OCCURRENCE OF STRONGYLOIDES IN AMERICAN SWINE

Aside from the brief references made by Ransom (13), Hall (5),

and Sandground (15) to the occurrence of Strongyloides in American swine, there appear to be no published data concerning these parasites of domestic swine in the United States. In view of the recorded pathogenicity of Strongyloides, especially to young pigs, based on a study of clinical symptoms of infested animals by Perroncito (10), Reisinger (14), and Marotel (8), it appears important to determine whether a presumably important pathogenic parasite of young pigs has been overlooked by most American parasitologists. As a pre-liminary step to an exper-

parasitologists. As a preliminary step to an experimental study of the pathogenicity of Strongyloides for pigs, it appeared essential to determine: (1) Whether one or more than one species of Strongyloides has been recorded from these host animals; and (2) whether the view shared by certain helminthologists with reference to the probable identity of S. papil-losus and S. suis is supported by morphological and other evidence. Examinations of pigs at

Examinations of pigs at the Bureau of Animal Industry Experiment Station, Bethesda, Md., for the presence of Strongyloides were begun by the senior author in 1927. Cultures of feces from young pigs, from a few weeks to a few months old, revealed, after about 24 hours, the presence of rhabditiform larvae, and after 48 hours or longer the presence of filar-

500 H FIGURE 1.—Strongyloides ransomi; parasitic female. a., anus; a. o., anterior ovary; int., intestine; n. r., nerve ring; es., esophagus; p. o., posterior ovary; ut., uterus; v., vulva

iform larvae and of free-living males and females, the number of males present being very few as compared with the number of females. In the course of post-mortem examinations of young pigs, which were killed at various times in connection with certain experiments, parasitic females belonging to the genus Strongyloides were obtained from the small intestine. An examination of these specimens showed that they differed in several important respects from S.

papillosus of sheep and also from the figures and descriptions of S.

suis published by investigators in Europe.

In the course of necropsies on three young pigs at Moultrie, Ga., by E. B. Cram and E. W. Nighbert, of the Zoological Division, several slender nematodes were collected from the small intestine and forwarded to the senior author for determination. Unfortunately these worms were poorly preserved, so that when they were examined no morphological details could be made out, but the shape of the tail resembled that in figures of Strongyloides from pigs published by European workers. The female tail which is figured and described by Reisinger and figured in Fiebiger's textbook on parasitology is highly attenuated, in contrast to the conical tail with a more or less blunt tip found in all specimens of Strongyloides collected from swine at Bethesda. A recent restudy of the latter forms by the writers and a comparison of these forms with those from sheep showed that the swine form represents a species distinct from the sheep form and also distinct from the pig form as figured and described from Europe. The name S. ransomi is proposed for the American species, the name S. suis being retained for the time being for the forms with acutely pointed tails. The latter species probably occurs in this country, as forms resembling it were collected from swine at Moultrie, Ga.

Strongyloides ransomi, new species.

Specific diagnosis: Strongyloides:

Parasitic females (fig. 1). From 3.33 to 4.49 mm. long and from 54μ to 62μ wide. Body long, filiform, and of nearly equal thickness from the region of the base of the esophagus to the region of the posterior ovarian loops. Beginning at about the region of the base of the esophagus, the body narrows gradually toward the anterior end, the head being attenuated to a diameter of about 15μ . Posteriorly the body diminishes in size backward. The diameter of the body in the region of the anus is from 23μ to 31μ . In the region of the posterior ovarian loops the body narrows considerably and becomes gradually reduced behind the anus, terminating in a distinctly tapering, conical tail, the tip of which is more or less blunt. The esophagus is from 605μ to 883μ long by 47μ wide. The diameter of the body in the region of the base of the esophagus is from 47μ to 54μ wide. The anus is located at a distance of from 53μ to 83μ from the posterior end. The vulva is a transverse slit, with salient lips, situated posterior to the middle of the body but considerably anterior to the last third of the body, at a distance of from 1.1 to 1.6 mm. from the tip of the tail. The ovary is twisted in loops anteriorly and is less constantly looped posteriorly. The posterior ovary is not uncommonly bent in a hairpin fashion, with a tendency to cross over and form a loop. (Fig. 2.) The eggs (fig. 3) are ellipsoidal, thin shelled, from 45μ to 55μ long, 26μ to 35μ wide, and contain an embryo at the time that they are eliminated with the feces.

Table 1 gives a summary of the measurements of eight specimens of parasitic females.

Table 1:—Measurements of eight specimens of parasitic females of Strongyloides ransomi

Size		Esophagus		Location of vulva		T	
Length	Width	Length	Width		From pos- terior end		
Mm.	μ	μ	μ	Mm.	Mm.	μ	
4.495	62	853	47	2. 821	1.674	μ 79	
3.72	54	760	47	2, 325	1.395	67	
4.03	62	605	47	2, 968	1. 162	68	
4. 65	. 62	853	47	2. 99	1.66	83	
3. 332	62	713	47	1. 922	1.41	71	
3. 952	62	822	47	2. 821	1. 131	67	
3, 689	62	883	47	2, 124	1. 565	67 53	
3. 67	62	775	47	2. 245	1.425	79	

Free-living generation:

Males (figs. 4 and 5). From 868μ to 899μ long and 54μ wide. Body of nearly equal diameter except in the tail region. Posterior to the anus the body becomes considerably narrowed, tapering gradually and terminating in a relatively long, slender tail; anteriorly the body narrows gradually, commencing

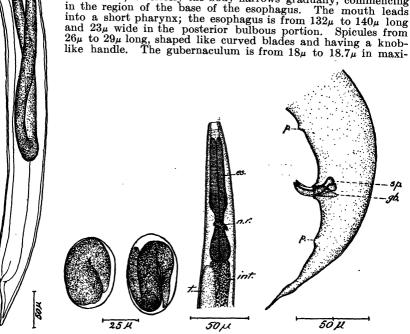


FIGURE 2.gyloides ransomi; posterior end of parasitic female

-Stron- FIGURE 3. loides ransomi

gyloides ransomi; anterior end of male. int., intestine; n. r., nerve ring; es., esophagus; t., testis

-Eggs of Strongy- Figure 4.—Stron- Figure 5.—Strongyloides posterior end of male. gb., gubernaculum; p., papilla; sp., spicule

mum diameter, and 9.4μ in minimum diameter. One preanal and one postanal papilla, ventral in position, approximately equidistant from the anus. is from 83μ to 90μ long.

Females (fig. 6). From 1 to 1.1 mm. long and 62μ wide in the region of the The body tapers very gradually anteriorly and narrows to a diameter of about 13μ to 15μ in the head region; the diameter of the body in the region of the esophagus is from 43μ to 47μ . Posteriorly the body tapers more abruptly than anteriorly, becoming considerably narrowed in the region of the rectum and tapering gradually to a slender tail. The diameter of the body in the region of the anus is about 23μ . The mouth leads into a short pharynx; the esophagus is from 124μ to 155μ long and 23μ wide in the posterior bulb. The vulva has salient lips and is located near the middle of the body. In young forms comparatively few ovarian eggs are present in the uterus, but in gravid females numerous shelled eggs are contained in the anterior and posterior uteri. After oviposition is completed the uterus shrinks in size and the ovaries appear to be degenerated. tail is from 150μ to 158μ long.

Rhabditiform larvae:

The rhabditiform larvae (figs. 7 and 8) are from about 280μ to somewhat over 400μ long and about 20μ in maximum width, the smaller forms being newly hatched. The pharynx is short, from 5μ to 6μ long. The esophagus is from about 70μ to nearly 90μ long. The genital primordium, which is about 15μ to 18µ long, is located approximately in the region corresponding to that of the middle of the intestine. The tail is tapering, about 55μ long.

Filariform larvae:

These larvae (fig. 9) are from 504μ to 635μ long and from 15μ to 19μ wide in the region of the base of the esophagus. The esophagus is from 240μ to 310μ

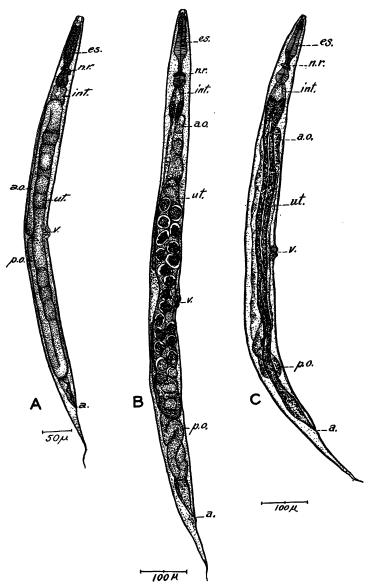


FIGURE 6.—Strongyloides ransomi: A, Young female; B, gravid female; C, female after oviposition. a., anus; a. o., anterior ovary; int., intestine; n. r., nerve ring; es., esophagus; p. o., posterior ovary; ut., uterus; v.. vulva

long and from 7.5μ to 11μ wide. The tail is tapering from 60μ to 90μ long. The genital primordium is located at a distance of from 168μ to 225μ from the tip of the tail, approximately in the region corresponding to that of the middle of the intestine.

Host.—Sus scrofa domestica.

Location.—Small intestine (embedded in mucosa). Free-living generation and rhabditiform and filariform larvae may be cultured in feces of infested hosts. Location.—Small intestine (embedded in mucosa). Type locality.—Bethesda, Md.

Type specimen of parasitic female.—Bureau of Animal Industry helminthological collection, United States National Museum No. 28779.

n.r.

Paratypes of parasitic female.—Bureau of Animal Industry helminthological collection, United States National Museum No. 28780.

Type specimens of free-living male and female.—Bureau of Animal Industry helminthological collection, United States National

Museum No. 28777.

Paratypes of free-living male and female.

Bureau of Animal Industry helminthological collection, United States National Museum No. 28778.

This species is dedicated to the memory of the late Brayton Howard Ransom, who reported, for the first time, Strongyloides from swine in the United States and who carried out important experimental work on skin penetration by S. papillosus and on the experimental transmission of this species to

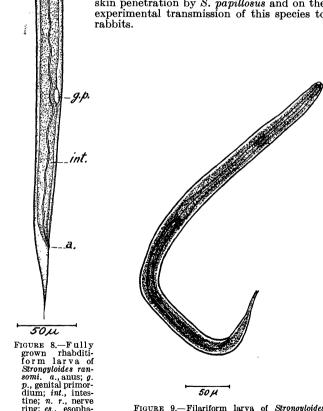
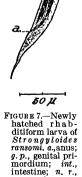


FIGURE 9.- Filariform larva of Strongyloides



nerve ring; es.,

int.,



COMPARISON OF STRONGYLOIDES RANSOMI WITH S. PAPILLOSUS

In a comparison of the parasitic females of Strongyloides ransomi with S. papillosus, the shape of the tail presents a striking difference. That of S. papillosus (fig. 10) is of fingerlike shape and markedly

blunt, whereas that of *S. ransomi* (fig. 11) is cone-shaped and tapers gradually, its tip being more or less bluntly rounded. Among numerous specimens of parasitic females from sheep and swine which were examined, the shape of the tail was found to be constant for each species, and the variations were not found to overlap. Aside from

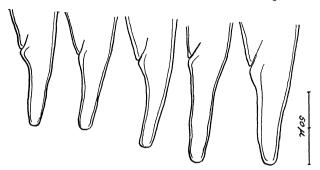


FIGURE 10.—Tails of parasitic females of Strongyloides papillosus

this conspicuous difference, no other highly significant morphological differences have been found in comparing the forms from the two hosts. As regards the size of the eggs, those of $S.\ ransomi$, obtained from fresh pig feces, showed a range of from 45μ to 55μ long by 26μ

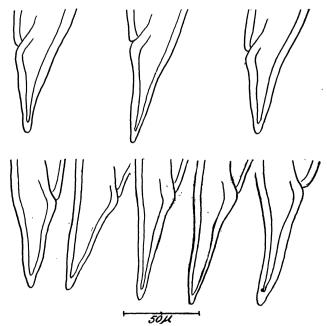


FIGURE 11.—Tails of parasitic females of Strongyloides ransomi

to 35μ wide, whereas those obtained from fresh sheep feces showed a range of from 48μ to 67.5μ long by from 30μ to 34μ wide. It is of interest to note that of 10 measured eggs of S. ransomi 8 were less than 50μ long and 2 were between 50μ and 55μ long, whereas 12 of 20 eggs of S. papillosus ranged from 60μ to 67.5μ in length, and only 1

egg was less than 50μ long, the remaining 7 eggs being between 52μ and 56μ long. In a general way the eggs of S. papillosus are longer

and more elongated than those of S. ransomi.

It is also noteworthy that whereas cultures of feces from swine infested with Strongyloides ransomi have yielded in all cases freeliving males, cultures of feces from sheep infested with S. papillosus have thus far failed to show the presence of males. Ransom (12) carried out a number of experiments on the transmission of S. papillosus from sheep to rabbits, and he apparently failed to find males in In 1911 he gives a fairly detailed description of the his cultures. free-living female and states that the male is undescribed. Baylis (1) states that the male of S. papillosus is apparently rare. He gives the first description of the free-living male of S. papillosus based on one specimen as follows: 750μ long by 35μ wide, tail 70μ long, spicules 35μ long. While the size measurements are consistently smaller than those recorded in this paper for S. ransomi, it is significant that the spicules of S. papillosus are considerably longer than those of S. ransomi, according to Baylis's measurements of those of the former The spicules of four specimens of S. ransomi showed the following lengths: 26μ , 28μ , 28μ , 29μ . It is to be regretted that Baylis does not give the host from the feces of which the male was One can not assume with absolute certainty that the host in question was a sheep, since Baylis lists the following hosts for

S. papillosus: Sheep, goat, ox, pig, and rabbit.

As regards the filariform larvae, 6 specimens of Strongyloides ransomi showed the following range in size: 503 µ long, 16 µ wide; 635μ long, 18μ wide; 519μ long, 18μ wide; 542μ long, 18μ wide; 519μ long, 16μ wide; 496μ long, 15μ wide. Seven filariform larvae of S. papillosus showed the following range in size: 651μ long, 17μ wide; 666 μ long, 15 μ wide; 681 μ long, 15 μ wide; 710 μ long, 15 μ wide; 651 μ long, 15 μ wide; 574 μ long, 15 μ wide; 666 μ long, 15 μ wide. While these measurements overlap, it is important to note that the filariform larvae of S. papillosus are considerably longer than those of S. ransomi, the maximum size of the latter being close to the minimum size of the The size of the esophagus of the filariform larvae in the two species shows a variation of from 230μ to 279μ in length by from 11μ to 15μ in width for S. papillosus, and a variation of from 240μ to 310μ in length by from 7.5μ to 11μ in width for S. ransomi. While these measurements overlap, it is important to note that the individual measurements of the esophagus for the two species show differences as follows: S. papillosus: 240μ by 11μ , 271μ by 11μ , 263μ by 11μ , 279μ by 15μ , 255μ by 11μ , 230μ by 11μ , and 279μ by 11μ ; S. ransomi: 255μ by 7.5μ , 310μ by 7.5μ , 240μ by 7.5μ , 263μ by 11μ , 263μ by 7.5μ , and 255μ by 7.5μ . Aside from the fact that the base of the esophagus of the filariform larvae of S. papillosus is wider in most specimens than that of S. ransomi, the ratio of the length of the esophagus as compared to the total length of the body is considerably larger in the The location of the genital primordium with reference to its distance from the anus in the two species is as follows: S. ransomi: 121μ , 125μ , 109μ , 118μ , 105μ ; S. papillosus: 147μ , 152μ , 170μ , 170μ , 170μ , 151μ , 165μ .

Aside from the morphological differences between S. ransomi and S. papillosus which have been noted, there also appears to be a biological difference between these two species, so far as concerns their ability to develop in the rabbit. As first shown by Ransom (12),

S. papillosus can develop to fertile maturity in rabbits. In order to determine whether there are any differences between S. ransomi and S. papillosus with regard to the degree of adaptability to various

abnormal hosts, the following experiments were performed:

Filariform larvae of S. ransomi were fed to a cat, a guinea pig, a rat, two rabbits, and a chick. These animals were held under observation for varying periods ranging from about three weeks to two months, during which interval the feces were examined for eggs and were cultured for the presence of larvae, with negative results in all cases. One rabbit in this series was fed filariform larvae on April 3,

1929; the animal died on April 24 and a careful examination failed to reveal the presence of Strongyloides in the intestine. The second rabbit was fed filariform larvae on May 7, 1929, and was killed on July 6; during this interval no eggs were detected in the feces and on post-mortem examination no Strongyloides were found

in the intestine.

Filariform larvae of S. papillosus were fed to two rabbits, two guinea pigs, and a chick. One rabbit, which was fed larvae on April 13 and 15, failed to show eggs in the feces up to May 10, on which day it was chloroformed. At necropsy 54 specimens of Strongyloides, most of which were not gravid, were collected from the intestine. The second rabbit was fed filariform larvae of S. papillosus on May 21, 1929; eggs were first noted in the feces of this rabbit on June 17 and continued to be eliminated with the feces up to July 8, during which interval several fecal examinations were Since July 11 the feces of this rabbit have been consistently negative for eggs, and cultures of the feces have failed to show the presence of larvae. The guinea pigs and chick were kept under observation more than six weeks, during which interval they showed no eggs in the feces; these animals showed no Strongyloides at necropsy.

It is evident from these experiments that S. papillosus can develop to fertile maturity in rabbits, while S. ransomi is apparently not adapted to this host.

STRONGYLOIDES SUIS

The status of the name Strongyloides suis still remains to be considered. As used by Von Linstow (6), this name has little, if any, zoological standing, as it is not accompanied by a description. Von Linstow apparently had in mind the species of Strongyloides from swine described by Lutz (7) which is described, however, without reference to specific details, the characters mentioned in the description being, with the exception of the size of the females, generic. For the time being, the name S. suis may be retained for the form described and figured by Reisinger (14) which, so far as can be judged from his illustration, appears to be identical with that figured by Fiebiger (2) from swine. Reisinger's species may be characterized as follows:

Parasitic females (fig. 12). From 4 to 6 mm. long by 80μ wide, attenuated at the anterior end. Esophagus one-fifth of the total length. Uterus contains



20 to 30 eggs. Vulva near the posterior fourth of the body. Eggs 60μ long by 40μ wide containing an embryo three and one-half to four times as long as the egg. Tail long and acutely pointed.

Reisinger failed to obtain the free-living generation in cultures. The forms which he figures as possibly representing the free-living males and females were obtained from feces in hogpens and are

unquestionably free-living nematodes.

The striking character of Reisinger's form is the acutely pointed tail, which so far as is known, and if accurately figured, is unique in the genus Strongyloides. The position of the vulva, approximately in the beginning of the posterior fourth of the body, represents another difference between this form and S. ransomi, in which latter the vulva in the parasitic female is located at some distance anterior to the beginning of the posterior third of the body.

anterior to the beginning of the posterior third of the body.

In view of the fact that Fiebiger's figure of Strongyloides from pigs, designated by him as S. longus, corresponds to that of Reisinger, at least so far as the shape of the female tail is concerned, and that forms resembling these worms were collected from pigs in Georgia, in which case it is to be noted that symptoms of digestive disturbance were observed and ascribed to these parasites, the recognition of these forms as a species distinct from S. ransomi is warranted. For the time being the name S. suis which has been used by many helminthologists for the species from swine may be retained for the longtailed European forms, largely as a matter of convenience. The retention of this name is also justified from the standpoint of nomenclature.

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